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RESULTS OF CROSSING *EUSCHISTUS VARIOLARIUS* AND *EUSCHISTUS ICTERICUS* WITH REFER- ENCE TO THE INHERITANCE OF TWO EXCLUSIVELY MALE CHARACTERS.

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The two exclusively male characters selected for study in this cross are first, the black or dark brown spot on the male genital segment of *Euschistus variolarius* and, second, the intro-mittent organ, which differs markedly in length in the two species.

In two recent papers¹ we described in detail the transmission of the above-mentioned exclusively male characters in a cross between *Euschistus variolarius* and *E. servus* and the results from the study of the transmission of these two characters in the cross of *E. variolarius* with *E. ictericus* are merely a confirmation of the results obtained from the cross of *E. variolarius* with *E. servus*. The results from the latter cross were published first because they were more satisfactory, for the reason that the spot which is so pronounced on the male genital segment of *variolarius* is entirely absent from the male segment of *E. servus*, whereas it is not entirely absent from the genital segment of *E. ictericus*. Although *ictericus* is described as having no spot on the genital segment, a faint spot is frequently present. This is not easily determined until the segment is pulled out and closely examined, but the spot, if present, can then be clearly seen, though it is not nearly so pronounced as that of *variolarius*. (Compare photos 61 and 62.) Although this spot is not a constant feature in *ictericus*, it is present often enough to make it impossible to determine how much of the inheritance of the

¹ "Results of Crossing *Euschistus variolarius* and *Euschistus servus* with Reference to the Inheritance of an Exclusively Male Character," *Journ. Linn. Soc. London, Zool.*, Vol. XXXII, 1914.

"Results of Crossing Two Hemipterous Species, with Reference to the Inheritance of Two Exclusively Male Characters," *Journ. Linn. Soc. London, Zool.*, Vol. XXXII, 1915.

spot in the hybrids is due to the female *variolarius* and therefore the results from this cross are less decisive, on this point, than the results from the cross with *servus*.

The intromittent organ, however, is a chitinous spiral which can be dissected out and accurately measured, making it possible to determine the exact size relations in the hybrid. We shall, therefore, first describe the results obtained from a study of the inheritance of this organ and shall then more briefly state the less definite results obtained from a study of the genital spot.

Dr. Eltringham's discovery of the difference in the length of the intromittent organ between the two species *E. variolarius* and *E. servus* (Foot and Strobell, '15) led us to expect a difference in the length of this organ between the two species *E. variolarius* and *E. ictericus*. The three species do, in fact, differ greatly in this character. At a magnification of twenty diameters, the mean length of the intromittent organ of *E. servus* is 166.41 mm. of *E. variolarius*, 96.70 mm. and of *E. ictericus*, 60.64 mm.

Our cross-breeding experiments with *variolarius* by *ictericus* differ in important details from our experiments with *E. variolarius* by *E. servus*. In the latter we succeeded in raising to maturity, eleven males and 16 females of the F₁ generation, and from these we were able to raise a large number of the F₂ generation (204 males and 249 females). In the *variolarius* × *ictericus* cross, on the contrary, we succeeded in raising only one specimen of the F₁ generation (a female). We were successful, however, in crossing this F₁ female with a pure *ictericus* male and we raised from this back-cross 76 males and 73 females. These results are a gratifying supplement to our cross-breeding experiments with *variolarius* and *servus*, for in the latter, a back-cross was commenced so late in the season that we were able to secure only 18 males and 8 females.

Details of Crossing Euschistus variolarius × *Euschistus ictericus*.—The three female *variolarius* used for this cross were hatched in our laboratory, and immediately after the fifth moult were caged with three male *ictericus* which were also hatched and reared in the laboratory. The parents of the three females were two of ten specimens of *variolarius* collected at White

Plains, N. Y., April 16, 1911, by Mr. de la Torre Bueno. These bugs were placed in a cage in our laboratory and, four days later, one pair mated, and while mating were transferred to a separate cage, in which they were kept during the entire breeding season, until the female died.¹

Three of the female offspring of this pair were used for the cross-breeding experiments with *ictericus*. They reached the winged stage on the following dates: July 3, one female reared from the group of 4 eggs deposited May 22; July 15, two females reared from the group of 29 eggs deposited June 9. The three male *ictericus* that were caged with these three *variolarius* females were reared from eggs deposited in our laboratory May 22 and June 2. These eggs were deposited in a cage containing ten *E. ictericus* specimens that had been collected a few days before by Dr. Knab in a swamp near Washington, D. C. One of the males from these eggs reached the winged stage July 7 and two, July 15 and the three were caged with the three above-mentioned *variolarius* females.

August 12 a pair of these bugs mated and while mating were transferred to a separate cage (cage 5). The record of this pair shows that they mated $6\frac{1}{4}$ hours² and did not mate again while they were under observation (from August 12 to November 24, 1911) when the female died. On August 15, 7 eggs were deposited, none of which developed. On August 18, 4 eggs were deposited one of which hatched and was raised to maturity—this being the F₁ female which we mated the following spring to a pure *ictericus* male. On August 25, 23 eggs were deposited, none of which developed. (See photo 63 for the male of this pair.)

A second pair mated August 19 and this pair also was isolated (cage 13). A group of 8 eggs was deposited by this second pair August 22 and a group of 18 eggs on August 25 but none of these 26 eggs developed.

¹ The record of the breeding period of this pair of *variolarius* was published in our report of the results of crossing *E. variolarius* × *E. servus*. This record is entered as "cage 2, 1911." Foot and Strobell, '14, *Journ. Linn. Soc. London, Zööl.*, Vol. XXXII, p. 362.

² The length of time for each mating can be given only approximately as observations were made not oftener than three or four times each hour, during the day and three or four times during the night.

The last pair of bugs of the original three pairs never mated, although they were kept under observation until October 11. They were then added to a cage containing eight specimens of the same cross (4 ♀ and 4 ♂) which we had caged to carry through the winter.

The record of the first pair shows that from August 15 to August 25, 34 eggs were deposited and that only one of these developed. If we add to these the above-mentioned 26 eggs from the second pair of this cross, we find that out of 60 *variolarius* eggs, that were presumably fertilized by *ictericus*; only one developed and hatched.

Comparing these results with those of the cross between *variolarius* × *servus*, we find that in the latter a very much larger proportion of eggs developed, for out of a total of 120 eggs, 37 developed and 32 of these hatched.

This contrast between the results of the two crosses is greatly increased if we add the number of eggs deposited by the *variolarius-ictericus* cross of the summer of 1912. As stated above we caged through the winter of 1911-12 five female *variolarius* and five male *ictericus*. All of these were reared in the laboratory from the same stock as those of the 1911 pairs. Only one of these mated the next season (cage 12, 1912). Of the 53 eggs which were deposited between June 11 and July 15 not one developed. We believe we might have had better success with wild males; but we failed in our efforts to get them in the spring of 1912. In summing the results we find that 113 eggs in all were deposited by the three *variolarius* females that were crossed with *ictericus* and that only one of these 113 eggs hatched; the remaining 112 did not show even the initial stages of development. This one egg that developed was deposited August 18 and was not hatched until August 28, as the weather was unseasonably cold. The nymph (a female) reached the winged stage September 26. We succeeded in keeping this hybrid in good condition through the winter of 1911-12, and the following June she mated with a pure *ictericus*. The record of this pair is as follows:

RECORD OF CAGE 3, 1912.¹

F₁ Hybrid ♀ (from *E. variolarius* × *E. ictericus*) and pure *E. ictericus* ♂—one pair.

June

- 15 3.45 P. M. mating. Continued to mate 17 hours.
 21 20 eggs (in two groups) 15 survived first moult.
 24 8 eggs. 7 hatched.
 28 6 eggs. 5 hatched.
 29 13 eggs. 12 hatched.

33 reared to winged stage (16♂ and 17♀).

When some of the nymphs from the above four sets of eggs reached the third or fourth moult, they were transferred to a large cage and therefore some specimens from each of these four sets were combined and thus the individuality of each set was lost.

July

- 5 12 eggs. 10 hatched. 9 reared to winged stage (3♂ and 6♀).
 6 14 eggs. All hatched. 13 reared to winged stage (5♂ and 8♀).
 8 7 eggs (on wire top of cage) } 12 hatched. 9 reared to winged stage (2♂
 9 6 eggs (on wire top of cage) } and 7♀).
 12 12 eggs. (5 of them on wire top of cage) 10 hatched. 9 reared to winged stage (5♂ and 4♀).
 16 8 eggs. All hatched. 7 reared to winged stage. 5♂ and 2♀.
 21 5 A. M. 6 eggs (on wire top of cage). All hatched. All reared to winged stage. (4♂ and 2♀).
 21 5 A. M. mating. Continued to mate 21 hours.
 24 18 eggs. All hatched. 16 reared to winged stage. (8♂ and 8♀).
 30 22 eggs (in 5 groups). 21 hatched. 18 reared to winged stage. (10♂ and 8♀.)

August

- 6 5 eggs }
 9 6 eggs } All hatched. 9 reared to winged stage. (5♂ and 4♀).
 13 14 eggs (in 4 groups). 12 hatched. 8 reared to winged stage. (5♂ and 3♀).
 17 12 eggs (in 2 groups). 11 hatched. Later added to nymphs from eggs deposited August 28.
 22 3.30 P. M. mating. Continued to mate 48 hours.
 28 6 eggs (scattered on wire top of cage). 5 hatched. Later added these to nymphs from eggs deposited August 17. 12 reared to winged stage. (8♂ and 4♀).
 30 Killed both the male and female. Both were inert and apparently nearly dying. (The female has had only four legs since July 12.) Preserved in glycerine (tube 33). See photo 64 for the male.

All the females of this pair and 20 males are preserved as pinned specimens; the rest of the males are preserved in glycerine. See photos 65-69 for twenty-five specimens.

¹ The data of this record are taken from our notes from which we have selected only the essential items, omitting such details as the dates of hatching, the dates when the five moults occurred and the number of nymphs that survived each moult. The eggs hatch from five to seven days after deposition, this variation depending largely on the temperature.

A comparison of the above record with those of pure *variolarius* shows that in this back-cross the relation between mating and deposition of eggs is not normal, for, as a rule, eggs are deposited not oftener than once or twice between two matings, whereas in this cross, eggs were deposited eleven times between the first two matings and six times between the last two matings. The number of eggs, however, that were deposited between June 21 and August 28 is above our average for pure *variolarius* and a normal proportion of these eggs developed. 195 eggs were deposited and 177 of these hatched. 149 were reared to the winged stage. (76♂ and 73♀.) All of these females are preserved as pinned specimens and the males are preserved either as pinned specimens or in glycerine.

Intromittent Organ.—This organ is a chitinous spiral easily dissected from the genital segment of the males (photos 1 to 60).

In accordance with Dr. Eltringham's suggestion, the entire male segment was first softened in warm caustic potash, until the intromittent organ was sufficiently pliable to be dissected out without breaking.

Only a single organ was mounted on a slide, and the slide was so indexed that the insect from which the organ was taken could be identified and therefore, the relation of the intromittent organ to any other character could be satisfactorily studied in one and the same insect. This was possible in the case of the genital spot, for the genital segment of all the specimens which were preserved in glycerine had been photographed before the segment was removed for dissection.

Each intromittent organ being mounted in balsam, it was photographed at a magnification of 20 diameters, and all measurements were made from these photographs. The actual length, therefore, of each organ is one-twentieth of the length recorded in this paper.

Measurements from such photographs of the intromittent organs of *E. variolarius*, *E. ictericus* and of the offspring from the back-cross are given in the following three tables.

Table I. gives the lengths of the intromittent organs of 62 specimens of *E. variolarius*. This table is quoted from our report of results from the cross between *E. variolarius* and *E. servus*. (Foot and Strobell, '15, see footnote, p. 322.)

Table II. gives the lengths of the intromittent organs from 32 specimens of *E. ictericus*.

Table III. gives the lengths of the intromittent organs of 71 offspring from the back-cross of a pure *ictericus* male with the one F₁ female we succeeded in raising from crossing *E. variolarius* ♀ by *E. ictericus* ♂.

As the intromittent organ of *E. ictericus* is much shorter than

TABLE I.

Lengths of intromittent organs from 62 specimens of *Euschistus variolarius*

× 20 diams.

85.5 mm.....	1
87 mm.....	1
88 mm.....	1
89 mm.....	1
90 mm.....	1
91 mm.....	1
92 mm.....	2
93 mm.....	4
93.5 mm.....	1
94 mm.....	6
94.5 mm.....	2
95 mm.....	1
95.5 mm.....	2
96 mm.....	7
96.5 mm.....	1
97 mm.....	1
97.5 mm.....	1
98 mm.....	6
98.5 mm.....	1
99 mm.....	2
100 mm.....	7
100.5 mm.....	1
101 mm.....	4
102 mm.....	3
104 mm.....	1
104.5 mm.....	2
106 mm.....	1
<u>5,996</u> mm.....	<u>62</u>

Mean length = 96.70 mm.

TABLE II.

Lengths of intromittent organs from 32 specimens of *Euschistus ictericus* ×

20 diams.

54.5 mm.....	1
55 mm.....	1
58 mm.....	3
59 mm.....	1
60 mm.....	8
60.5 mm.....	3
61 mm.....	2
62 mm.....	6
62.5 mm.....	2
63 mm.....	3
64 mm.....	1
64.5 mm.....	1
<u>1,940.5</u> mm.....	<u>32</u>

Mean length = 60.64 mm.

that of either *E. variolarius* or *E. servus*, it was much less difficult to get an accurate measurement of the length of the organ in *ictericus* and this was true also of the offspring from the

back-cross. We used, however, the same method as for the longer and more complicated coils of *servus*, *i. e.*, photographing each intromittent organ at a magnification of 20 diameters, and measuring the photographs with a small pair of architect's dividers. (For details see Plates I.-III., p. 337.)

TABLE III.

Lengths of intromittent organs from 71 specimens of offspring from back-cross
i. e., F₁ ♀ (from *E. variolarius* ♀ × *E. ictericus* ♂) by *E. ictericus* ♂

× 20 diams.

60 mm.....	2
62 mm.....	2
62.5 mm.....	1
63.5 mm.....	1
64 mm.....	4
66 mm.....	8
66.5 mm.....	3
67 mm.....	1
68 mm.....	7
68.5 mm.....	1
69 mm.....	7
70 mm.....	10
70.5 mm.....	2
71 mm.....	3
72 mm.....	7
72.5 mm.....	2
73 mm.....	1
73.5 mm.....	1
74 mm.....	3
74.5 mm.....	1
75 mm.....	1
76 mm.....	2
76.5 mm.....	1
<u>4.897.5 mm.....</u>	<u>71</u>

Mean length = 68.97 mm.

Genital Spot.—A study of the inheritance of the genital spot in the offspring from the back-cross of *variolarius-ictericus* is of interest merely as furnishing additional data in support of the results given by the crosses of *variolarius* by *servus*. These results, however, are by no means as definite as those from the intromittent organ, for the dimensions of the genital spot can be only relatively stated, they cannot be accurately measured as in the case of the length of the intromittent organ. The in-

fluence of each parent in the transmission of the genital spot in the hybrids can, therefore, be ascertained only approximately and the case is further complicated in the *ictericus* cross by the fact that in *E. ictericus*, unlike *E. servus*, a genital spot is not wholly absent.

Photo 61 is of seven male specimens of *E. variolarius* showing on each genital segment, the brown or black spot characteristic of the *variolarius* male, and photo 62 is of seven specimens of *E. ictericus* showing the faint indication of a genital spot which is characteristic of nearly all *E. ictericus* males. As stated above, the spot, when present, is so indistinct that in most cases it is easily overlooked unless the segment is pulled out and closely examined, and this is perhaps why this species is described as having no spot on the genital segment. Van Duzee's description is as follows:

"*Euschistus ictericus* Linn.

"Found in the Northern States and Canada across the whole width of the continent. It is generally to be found on sedges in swampy spots or along the borders of streams or other bodies of water. It may be distinguished from the foregoing [*E. variolarius*] by the calloused ruga connecting the humeri which are more produced than in *variolarius*, and the genital segment of the male wants the black spot found in that species."¹

Although the presence of a faint spot in *ictericus* is an embarrassing factor in comparing the results of the *variolarius-ictericus* cross with those of the *variolarius-servus* cross, it by no means obscures the fact that the evidence from the two crosses is in complete harmony.

The *servus* crosses demonstrated that the genital spot was transmitted through the female of the first cross, and this is supported by the *ictericus* back-cross. The inheritance from the *variolarius* female of the first cross can be appreciated by comparing the faint spot of the pure *ictericus* specimens of photo 62 with the spot in some of the back-cross offspring, for example the first specimen of photo 65, the second specimen of photo 66, the third and last specimens of photo 69. In these the spot is almost as strong as that of the pure *variolarius* males and much

¹ Our *Euschistus ictericus* specimens were identified by J. R. de la Torre Bueno.

stronger than any of the genital spots of the pure *ictericus* males.

The *variolarius-servus* crosses further demonstrated that the genital spot was transmitted directly from the male and this is also supported by the *variolarius-ictericus* back-cross. The *ictericus* inheritance is shown in all the photographed specimens in which the spot is quite as insignificant as the faintest spot in the pure *ictericus* specimens.

Although the harmony in results with those of the *servus* experiments is evident, the factor of an indefinite spot in *ictericus* makes a detailed comparison less satisfactory and for this reason we shall discuss the results from the two back-crosses in relation to the intromittent organ rather than the genital spot. These two exclusively male characters (as we demonstrated by the *servus* crosses) give exactly the same evidence, in every detail, in their bearing on current theories under discussion.

RESULTS AND DISCUSSION.

The results obtained from this back-cross, $F_1 \text{ } \varnothing$ (from *variolarius* \times *ictericus*) by *ictericus*, are so nearly a repetition of those obtained from the back-cross of $F_1 \text{ } \varnothing$ (from *variolarius* \times *servus*) by *variolarius*, that they would seem scarcely to merit separate publication: but for the fact that the results obtained from the few specimens secured from the latter cross were of small scientific value, until supported by more data, and such data (from *ictericus*) were not in shape for publication when the results of the *servus* cross went to press.

One point of interest in the back-cross of $F_1 \text{ } \varnothing$ by *variolarius* was that the offspring did not show a Mendelian type of inheritance, but that the length of the intromittent organ appeared to be a quantitative response to the proportion of inheritance from the two species.

In attempting to measure the strength of the inheritance in this cross, we found that the effect on the length of the organ corresponded almost exactly with the relative amount of *variolarius* to *servus* in the offspring. This was 3 *variolarius* to 1 *servus*, as *variolarius* was first crossed with *servus* and a male *variolarius* used for the back-cross with the F_1 female. In our report of this cross we stated the results as follows:

"If we measure the amount of the *variolarius* inheritance in this back-cross, we find an astonishing agreement between the theoretical expectation and the actual result. The relative amount of *variolarius* to *servus* in the offspring of this back-cross is 3 to 1, and we should expect, therefore, the mean length of the intromittent organ of *servus* to be reduced by 75 per cent. of the difference between the mean lengths in *variolarius* and *servus*. This difference is 69.71 mm., 75 per cent. of this being 52.28 mm. Deducting this from the mean length of the organ of *servus* (166.41 mm.) would leave 114.13 mm. as the mean length of the organ of the offspring from this back-cross. The mean length is in fact 113.47 mm., this being only 0.66 mm. less than the calculated expectation."¹

If our results had followed a Mendelian type of inheritance, assuming the *servus* length of organ to be dominant, we should expect the mean length of the intromittent organ to be approximately 131.33 mm. instead of being the above simple expression of the proportion of inheritance from the two species.

This result would seem scarcely to merit serious consideration, as it was based on the inheritance from only 18 males; but from the back-cross reported in the present paper (*variolarius-ictericus*) we succeeded in getting 76 males and these repeat the evidence given by the 18 males of the first experiment.²

The two experiments are entirely similar except that in the first experiment the back-cross was made with a male of the same species as the female of the first cross (*variolarius*) and in the second experiment the back-cross was made with a male of the same species as the male of the first cross (*ictericus*).

If we look for an agreement in results from the two experiments, we should expect the mean length of the intromittent organ of the 71 males from the second back-cross to show a like quantitative response in inheritance to that in the case of the 18 males of the first experiment.

In this second back-cross we have 3 parts *ictericus* to 1 *variolarius*, and we should expect the mean length of the intromittent

¹Foot and Strobell, '15, "Results of Crossing Two Hemipterous Species with Reference to the Inheritance of two Exclusively Male Characters," *Journ. Linn. Soc. London, Zoöl.*, Vol. XXXII., p. 474, 1915.

²The intromittent organs of 71 of these 76 males were measured. See page 329.

organ of *variolarius* to be reduced by 75 per cent. of the difference between the mean lengths in *ictericus* and *variolarius*. This difference is 36.06 mm., 75 per cent. of this being 27.04 mm. Deducting this from the mean length of the organ of *variolarius* (96.70 mm.) would leave 69.66 mm. as the mean length of the organ from this back-cross. The mean length is in fact 68.97 mm., this being 0.69 mm. less than the calculated expectation. In both back-crosses the slightly stronger inheritance is in favor of the shorter type of intromittent organ and from the species giving 75 per cent. of the inheritance.

The 71 males from this back-cross further support the results of the first experiment as follows:

The back-cross (*variolarius-servus* by *variolarius*) showed that the length of the intromittent organ was transmitted directly from the male and also indirectly through the female, and that therefore the so-called male- and female-producing spermatozoa do not differ functionally in their transmission of a character so exclusively male as the intromittent organ.

Its direct transmission by the male was proved by the decrease in the mean length of the organ of the offspring from the back-cross as compared with that of the F_2 hybrids and it is further shown by the F_1 generation of the *variolarius-servus* crosses. The facts are as follows:

Mean length of the organ—

In the <i>variolarius</i> species	96.70 mm.
In the <i>servus</i> species	166.41 mm.
In the F_1 hybrids	124.9 mm.
In the F_2 hybrids	124.42 mm.
In the offspring from the back-cross	113.47 mm.

The *increase* in the mean length of the organ in the F_1 hybrids as compared with that of the *variolarius* species proves the direct transmission from the male parent, and the *decrease* in the mean length of the organ in the offspring from the back-cross as compared with that of the F_1 and F_2 generations shows again the direct influence of the male parent, the *servus* male of the first cross increasing the length towards that of the *servus* species and the *variolarius* male of the back-cross reducing it towards the *variolarius* species.

These results are supported by the *variolarius-ictericus* back-

cross though the evidence of the *direct* influence of the male parent might be questioned in this cross, as we did not succeed in securing any F₁ or F₂ males, and this would leave open the question whether the *ictericus* inheritance in these offspring was due in part to direct inheritance from the male of the back-cross or wholly due to indirect inheritance through the F₁ female. In the *servus* experiments, on the contrary, the direct influence of the male in both the first cross and the back-cross is beyond question.

Evidence of the transmission of this exclusively male character through the female is given in both back-crosses, but in the *variolarius* by *servus* experiments it is most conclusively shown by the mean length of the intromittent organ of the F₁ generation, where the inheritance from the pure *variolarius* female of the first cross is clearly in evidence.

In the *ictericus* experiment, the inheritance from the pure *variolarius* female of the first cross is shown in the increased mean length of the intromittent organ of the offspring of the back-cross as compared to that of the pure *ictericus* species. The facts are as follows:

Mean length of the organ—

In the <i>variolarius</i> species	96.70 mm.
In the <i>ictericus</i> species	60.64 mm.
In the offspring from the back-cross	68.97 mm.

A further point for consideration in the two back-crosses is the fact that in the first (*variolarius-servus*) the 25 per cent. inheritance is from the *male* of the first cross (*servus*) and in the second (*variolarius-ictericus*) the 25 per cent. inheritance is from the *female* of the first cross (*variolarius*). As in the one case, this one quarter inheritance was received directly from the male (*servus*) and in the other case indirectly through the female (*variolarius*), and as these have so nearly the same value in the offspring from both back-crosses, we would seem to have the strongest evidence that the so-called male- and female-producing spermatozoa do not differ quantitatively in their transmission even of a character so exclusively male as the intromittent organ.

In the *variolarius-servus* by *variolarius* back-cross we have direct evidence that this exclusively male character—the length of the intromittent organ—is transmitted by the so-called female-

producing spermatozoa, for the *servus* inheritance is from the F_1 female, which must have developed from an egg fertilized by a female-producing spermatozoön of *servus*.¹

Thus the evidence that not only the so-called male-producing spermatozoa but also the so-called female-producing spermatozoa can transmit even such an exclusively male character as the intromittent organ, and the fact that these so-called sex-determining spermatozoa do not differ functionally in the transmission of such a character certainly justifies much scepticism as to that sex-determination hypothesis which is based on the assumption of male- and female-producing spermatozoa.

In the reports of our *variolarius* by *servus* experiments we have repeatedly discussed the bearing of the results on the interesting and ingenious hypotheses which attempt to locate Mendelian factors not only in the chromosomes as such, but in definite chromosomes and in definite areas of definite chromosomes, and we have pointed out that the evidence from our results was in direct contradiction to such hypotheses and, further, that the evidence, as stated above, was against the hypothesis that assigned the rôle of sex-determination to the "sex-chromosomes" of the so-called male- and female-producing spermatozoa. As the evidence bearing on these questions is simply repeated in this *variolarius* by *ictericus* cross, we would (to avoid repetition) refer our readers to a recent paper² where we have briefly discussed the evidence in relation to these questions.

We feel almost like apologizing for our persistent criticism of these ingenious chromosome hypotheses so brilliantly launched by Morgan and his pupils³ and so vigorously advocated by Wilson.⁴

Our scepticism was perhaps primarily due to fourteen years' patient study of the chromosomes of *Allolobophora fætida*, these

¹ For the sake of the argument we must assume, for the moment, the existence of male- and female-producing spermatozoa.

² Foot and Strobell, *Journ. Linn. Soc.*, London, 1915, pp. 475-486.

³ A complete list of the literature by Morgan and his pupils is given in their recent volume, "Mechanism of Mendelian Heredity," Morgan, Sturtevant, Muller and Bridges. Henry Holt & Company, 1915.

⁴ A forceful presentation and endorsement of these hypotheses was recently given by Wilson in his Croonian Lecture. *Proceedings Royal Soc.*, ser. B, Vol. LXXXVIII., No. B 603.

years of investigation of one form forcing us to the conviction that the chromosomes share a variability that is admittedly a characteristic of other organs of the cell and a characteristic of all organic structures. Such convictions as to the morphological nature of the chromosomes made it impossible to have faith in any hypotheses that were based on the type of individuality of the chromosomes demanded by the theories in question.

In a recent paper, Trow¹ gives an able and searching criticism of one of these hypotheses and he has the sympathy of all sceptics when he voices the pressing need of an accurate knowledge of the chromosomes, especially of the maturation divisions where alone can be found the cytological support essential to a foundation for such a superstructure of imaginary architecture. This need is further voiced by Bateson² in his report on a recent volume by Morgan and his pupils.³ Of the maturation prophases he says: "That twisting takes place in many types, especially *Amphibia*, is clear; but neither the figures reproduced from Janssens nor the originals from which they are taken—still less the very fragmentary observations of both Stevens and Metz from *Drosophila*—provide more than a slender support for this most critical step in the argument. It is to be hoped that the authors will before long tell us exactly upon what evidence they are here relying."

It is well known by cytologists that, with our present methods of technique, an accurate knowledge of the maturation divisions of *Drosophila* is impossible and one is led to suspect that this ignorance as to the chromosomes leaves the imagination a freedom that perhaps would not be possible if curbed by more hard facts.

¹ "A Criticism of the Hypothesis of Linkage and Crossing Over," *Journ. Genetics*, Cambridge, England, Vol. 5, No. 4, 1916.

² *Science*, N. S., Vol. XLIV., No. 1137, p. 536.

³ "The Mechanism of Mendelian Heredity."

EXPLANATION OF PLATES I.-III.

We photographed each intromittent organ at a magnification of 20 diameters and prints on matte paper were made from these negatives. Then each subject was accurately measured with a small pair of architects' dividers fitted with no. 9 needle points, and set at 2 mm. The measurements were made on the matte prints so that each division of 20 mm. could be indicated by a pencil mark and numbered. The measurements were taken from the distal end of the intromittent organ to the point where the thick part of the coil enters the gland. The coil is most easily dissected off at this point (*e. g.*, photos 3, 5, 6, 8, etc.) but in those cases where part of the canal within the gland has been preserved (*e. g.*, photos 1 and 2) the point from which the measurement was made may be readily determined, for the part within the gland is transparent and quickly tapers to a finer canal which apparently extends through the entire gland. The transparency of that portion of the canal within the gland is much clearer in the preparations than in the photographs, for when the chitin has a yellow tinge it appears black and opaque in the photograph.

In many specimens we have left a small piece of the gland at the point where the intromittent organ enters (*e. g.*, photos 7, 9, 10, 12, 14, 19, etc.).

PLATE I.

PHOTO 1. Intromittent organ of *Euschistus variolarius*—the father of the *E. variolarius* female that was fertilized by the pure *E. ictericus* male.

Length of intromittent organ 96 mm.

PHOTOS 2, 3 and 4. Intromittent organs of three brothers of the *E. variolarius* female that was fertilized by the pure *E. ictericus* male. From this cross we raised the F₁ female which was back-crossed with a pure *E. ictericus* male and produced the offspring described in this paper.

Length of the intromittent organ of photo 2, 100 mm.—of photo 3, 94 mm.—of photo 4, 99 mm.

PHOTOS 5 to 8. Typical specimens of the intromittent organ of *Euschistus variolarius*.

Length of the intromittent organ of photo 5, 93 mm.—of photo 6, 93.5 mm.—of photo 7, 97.5 mm.—of photo 8, 98 mm.

PHOTO 9. Intromittent organ of the *Euschistus ictericus* of the original cross (cage 5, p. 324). This male *ictericus* was raised in our laboratory and fertilized the *Euschistus variolarius* female from which we obtained the F₁ female used for our back-cross experiment.

Length of the intromittent organ 60 mm.

PHOTO 10. Intromittent organ of the *Euschistus ictericus* that fertilized the F₁ female . . . (the father of all the offspring from our back-cross experiment). (See record, p. 326.)

Length of the intromittent organ 63 mm.

PHOTOS 11, 12 and 13. Intromittent organs of three of the original stock of *Euschistus ictericus* that we received from Washington, D. C., May 18, 1911.

Length of the intromittent organ of photo 11, 62 mm.—of photo 12, 60 mm.—of photo 13, 62.5 mm.

PHOTO 14. Intromittent organ of an *E. ictericus* male that was raised in our laboratory in 1911, kept through the winter, and in 1912 mated with a pure *E. variolarius* female. (See account of cage 12, p. 325.)

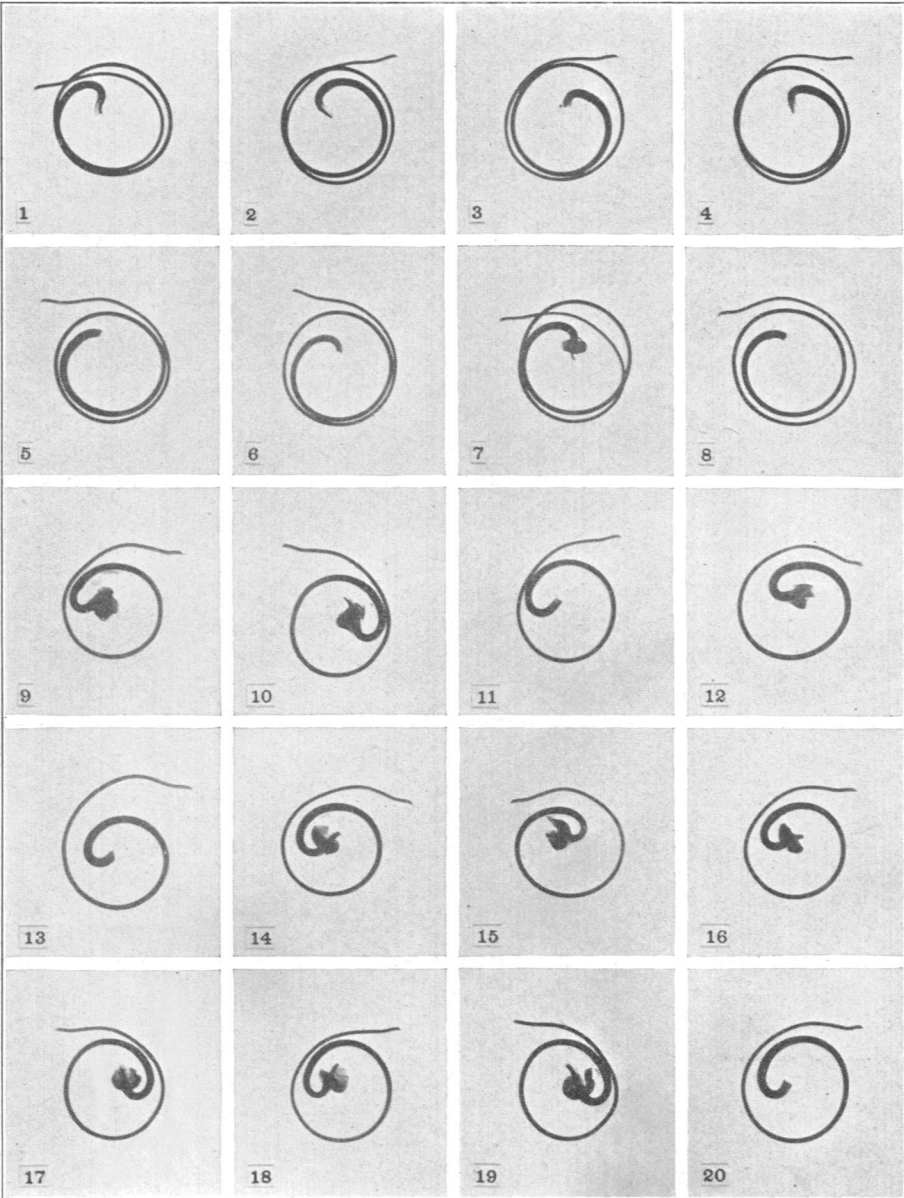
Length of the intromittent organ 60 mm.

PHOTO 15. Intromittent organ from one of the brothers of the *E. ictericus* that was used for the original cross with *E. variolarius*. These were raised in our laboratory in 1911.

Length of the intromittent organ 54.5 mm.

PHOTOS 16 to 20. Intromittent organs from five typical *E. ictericus* males that were raised in our laboratory during the summer of 1911.

Length of the intromittent organ of photo 16, 58 mm.—of photo 17, 59 mm.—of photo 18, 60 mm.—of photo 19, 61 mm.—of photo 20, 64.5 mm.



K.F. & E.C.S. photo.

INTROMITTENT ORGANS of *E. VARIOLARIUS* & *E. ICTERICUS*

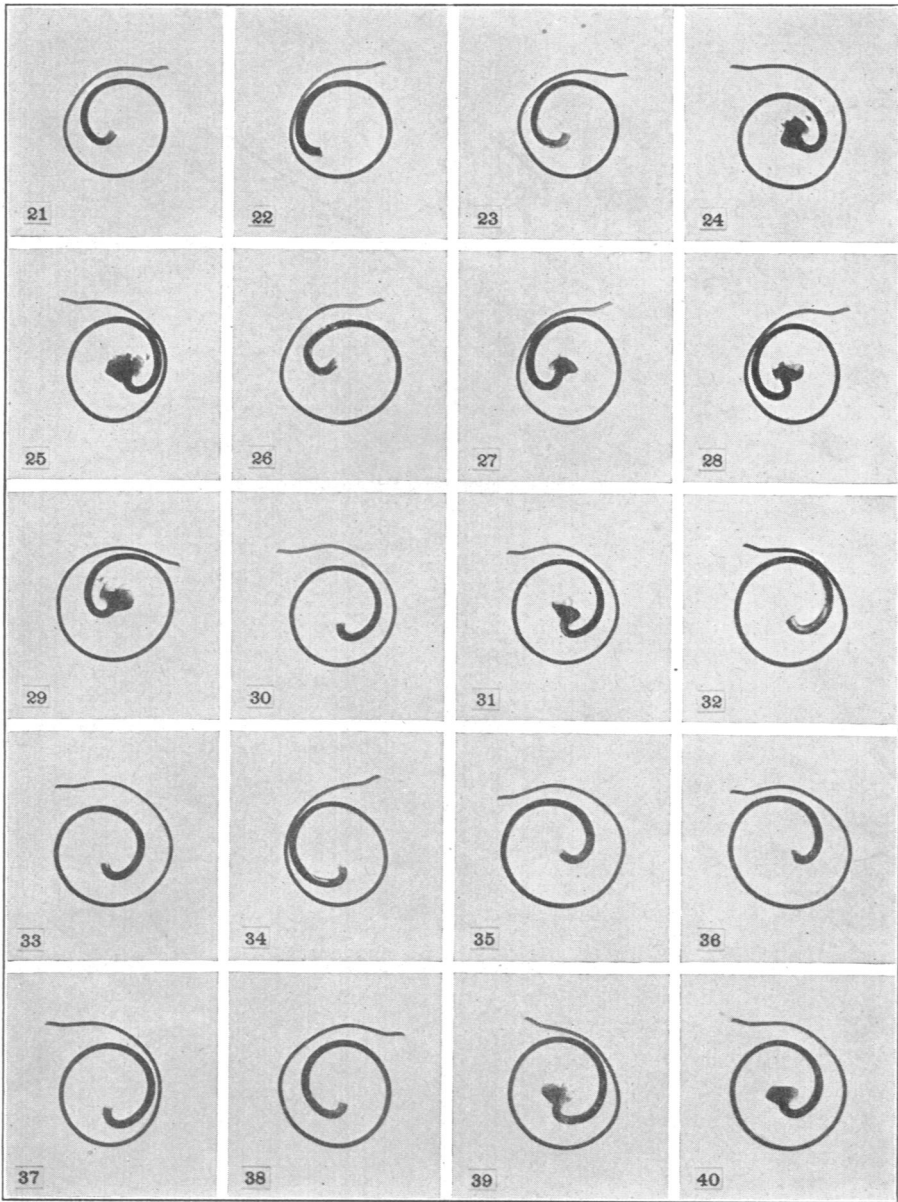
PLATES II AND III (PHOTOS 21-60).

The photographs of these two plates show typical intromittent organs from 40 of the 76 males which we succeeded in rearing from the back-cross with *E. ictericus* male and the F₁ female obtained from a cross with *E. variolarius* ♀ × *E. ictericus* ♂.

The photographs of these 40 intromittent organs have been placed on the plates in the order of their size, photo 21 being the shortest (60 mm.) and photo 60 the longest (76.5 mm.).

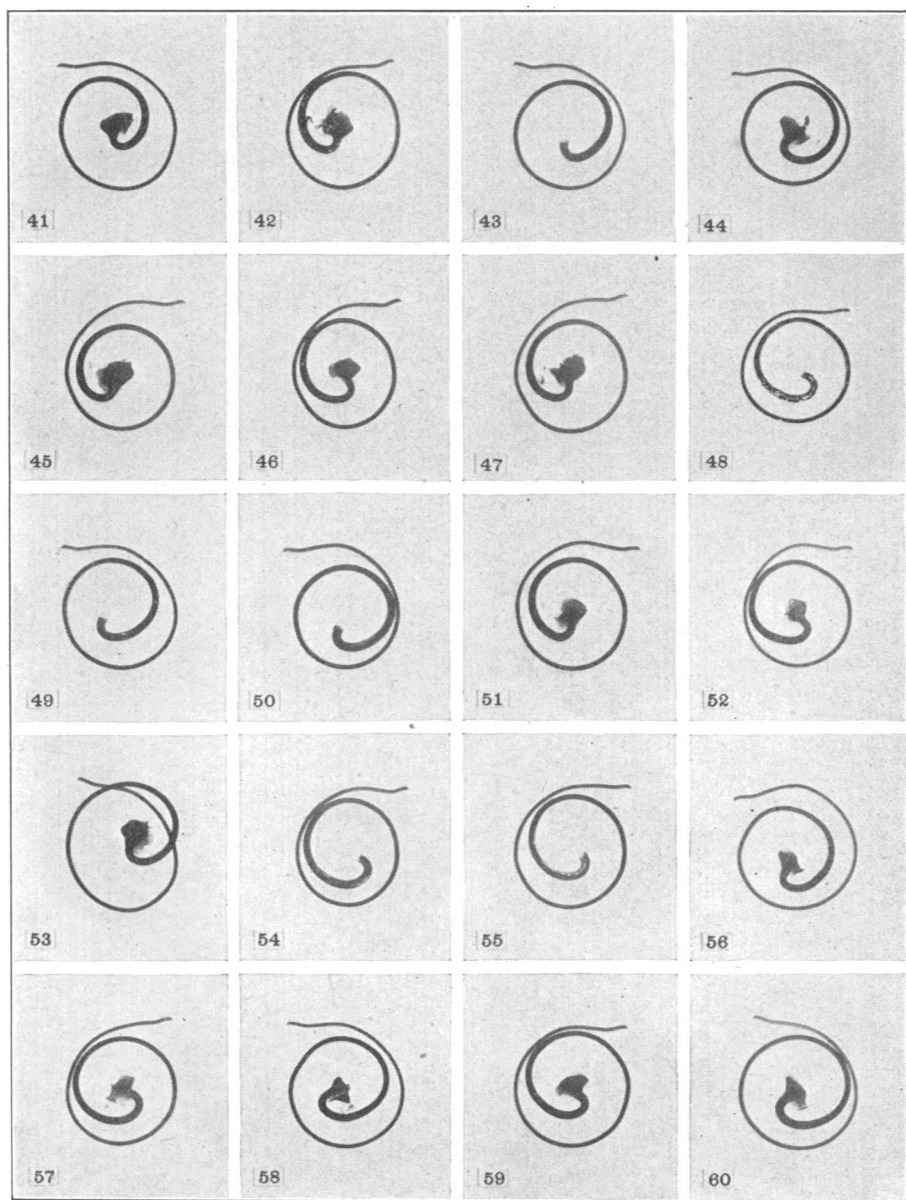
None of the 71 specimens which were measured can be classed with the *variolarius* intromittent organ which varies in length between 85.5 mm. and 106 mm. Ten of the 71, however, can be classed with the *ictericus* intromittent organ which varies in length between 54.5 mm. and 64.5 mm., though none of the specimens are as short as the shortest *ictericus* organ (54.5 mm.). The remaining 61 are variable intermediates.

The length of the intromittent organs of photos 21 to 60 is as follows: Photo 21, 60 mm.; Photo 22, 60 mm.; Photo 23, 62 mm.; Photo 24, 62 mm.; Photo 25, 62.5 mm.; Photo 26, 63.5 mm.; Photo 27, 64 mm.; Photo 28, 64 mm.; Photo 29, 66 mm.; Photo 30, 66 mm.; Photo 31, 66 mm.; Photo 32, 66.5 mm.; Photo 33, 67 mm.; Photo 34, 68 mm.; Photo 35, 68 mm.; Photo 36, 68 mm.; Photo 37, 68 mm.; Photo 38, 69 mm.; Photo 39, 69 mm.; Photo 40, 69 mm.; Photo 41, 69 mm.; Photo 42, 70 mm.; Photo 43, 70 mm.; Photo 44, 70 mm.; Photo 45, 70 mm.; Photo 46, 71 mm.; Photo 47, 71 mm.; Photo 48, 72 mm.; Photo 49, 72 mm.; Photo 50, 72 mm.; Photo 51, 72 mm.; Photo 52, 72 mm.; Photo 53, 73 mm.; Photo 54, 73.5 mm.; Photo 55, 74 mm.; Photo 56, 74 mm.; Photo 57, 75 mm.; Photo 58, 76 mm.; Photo 59, 76 mm.; Photo 60, 76.5 mm.



K.F. & E.C.S. photo.

INTROMITTENT ORGANS of the offspring from the BACK-CROSS, F₁ ♀ (from E. VARIOLARIUS × E. ICTERICUS) by E. ICTERICUS.



K.F. & E.C.S. photo.

INTROMITTENT ORGANS of the offspring from the BACK-CROSS, F₁ ♀ (from *E. VARIOLARIUS* × *E. ICTERICUS*) by *E. ICTERICUS*.

PLATE IV.

These photographs of the ventral surface of 41 male insects are of specimens preserved in pure glycerine in test tubes. The genital segment of each insect has been pulled out and cotton inserted behind the segment to hold it in position to show the entire ventral surface.

The magnification is about $1\frac{1}{2}$ diameters.

PHOTO 61. Seven male specimens of *E. variolarius*, showing the typical black spot on the genital segment. These are the same specimens which were photographed for our report of the cross between *E. variolarius* and *E. servus*.

PHOTO 62. Seven male specimens of *E. ictericus*, showing that the spot on the genital segment which is so pronounced in *E. variolarius* (photo 61) is only faintly indicated in *E. ictericus*.

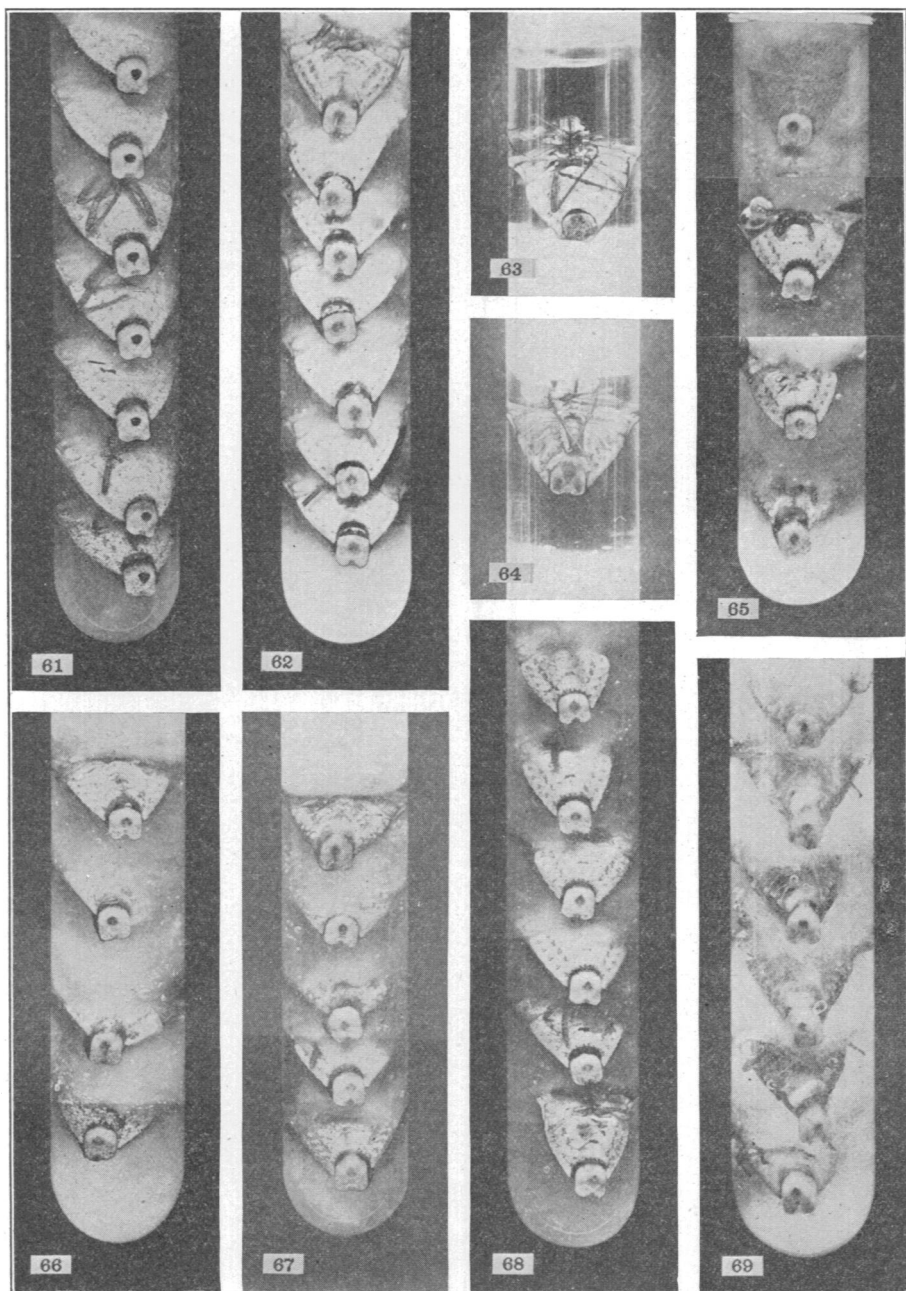
PHOTO 63. The *E. ictericus* male that fertilized the *E. variolarius* female of the first cross, p. 324. Photo 9 shows the intromittent organ of this insect.

PHOTO 64. The *ictericus* male that fertilized the F₁ female hybrid that was raised from the cross *E. variolarius* ♀ × *E. ictericus* ♂.¹ From this back cross (see Record, p. 326) 195 eggs were deposited and 177 of these hatched, 149 were reared to the winged stage (76 males and 73 females).

PHOTOS 65 to 69. Twenty-five specimens of the 76 males from the above mentioned back-cross.

A comparison of these 25 specimens with photo 62 shows the influence of the *E. variolarius* grandmother on the genital spot, for a few of these specimens have the genital spot almost as pronounced as that of the pure *variolarius* species and in the majority of the specimens the spot is stronger than that of the pure *ictericus* individuals of photos 62 and 63 and of the pure *ictericus* parent (photo 64). The *ictericus* inheritance is shown in those individuals which have merely a faint indication of the genital spot, *e. g.*, the lower three insects of photo 67 and the lower two of photo 68.

¹ The three apparently pigmented spots on the genital segment of this specimen are misleading,—they are in fact, a slight discoloration of the segment and not a pigmentation. The genital spot of this individual is like that of the lowest specimen of photo 67. Photo 10 shows the intromittent organ of this insect.



MALE SPECIMENS of *E. VARIOLARIUS*, *E. ICTERICUS* & offspring from the BACK-CROSS, F_1 ♀ (from *E. VARIOLARIUS* × *E. ICTERICUS*) by *E. ICTERICUS*.